

***Peregrinamor gastrochaenans* (Bivalvia: Mollusca), a New
Species Symbiotic with the Thalassinidean Shrimp
Upogebia carinicauda (Decapoda: Crustacea)**

Makoto Kato¹ and Gyo Itani²

¹ Graduate School of Human and Environmental Studies, Kyoto University,
Yoshida-Nihonmatsu-cho, Sakyo-ku, Kyoto, 606-8501 Japan

E-mail: kato@gaia.h.kyoto-u.ac.jp

² Seto Marine Biological Laboratory, Kyoto University,
Shirahama, Wakayama, 649-2211 Japan

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A new species of the hitherto monotypic bivalve genus *Peregrinamor* (Galeommatidae) was found attached to the ventral side of the cephalothorax of a small thalassinidean shrimp, *Upogebia carinicauda* (Stimpson, 1860) (Upogebiidae) collected from tidal flats of Amami-Oshima Island, Ryukyu Archipelago in Japan. The bivalve is dorso-ventrally flattened and pilfers suspended matter intercepted by the host's filtering basket. This new species, *Peregrinamor gastrochaenans*, can be discriminated from the type species of the genus, *P. ohshimai* Shôji, 1938, by its laterally more inflated shell with a permanent postero-ventral gape and by the expanded, fleshy posterior mantle protruding from the gape. Adaptations of the bivalve to the small host species and possible functions of the postero-ventral gape are discussed.

Key Words: symbiosis, Galeommatidae, *Upogebia*, tidal flat, *Peregrinamor*, new species, Japan.

Introduction

Many galeommatoidean bivalves have commensal relationships with other invertebrates (Ponder 1998). The genus *Peregrinamor* was first described within the Gaimardiidae by Shôji (1938), but later transferred to the Montacutidae (Kato and Itani 1995), a family which has since been synonymized with the Galeommatidae (Ponder 1998). The only species of the genus known until now, *Peregrinamor ohshimai* Shôji, 1938, is a rare bivalve that lives permanently attached to thalassinidean mud shrimps of the genus *Upogebia*. These shrimps construct U- or Y-shaped burrows in the mud and filter suspended matter by creating water currents in the burrows (MacGinitie 1930; Dworschak 1987; Griffis and Suchanek 1991). A single bivalve attaches itself to the ventral side of the cephalothorax of the mud shrimp by using its byssus, with a dorso-ventral and longitudinal orientation and the anterior part towards the head of the host (Kato and Itani 1995). The bivalve grows at a similar rate with its host, maintaining the ratio of shell length to host's carapace

length.

In tidal flats in Japan, at least six species of *Upogebia* are known to occur (Sakai 1982), some of which often coexist. While morphological and ecological traits vary among *Upogebia* species, the host range and host specificity of the symbiotic bivalve is still not clearly understood. Recent studies of these relationships have revealed a new *Peregrinamor* species symbiotic with *U. carinicauda* (Stimpson, 1860) from the Amami Islands in the Ryukyu Archipelago of Japan. This host species is widely distributed from the West Pacific to the Western Indian Ocean (Sakai and Takeda 1995), and it is much smaller than the *Upogebia* species that are hosts of *P. ohshimai*. In this paper, we describe this second species of *Peregrinamor* and discuss the adaptations of the symbiotic bivalve to the small host species.

Materials and Methods

We surveyed the symbionts of *Upogebia carinicauda* at several protected tidal flats in the Amami Islands, Kagoshima Prefecture. We collected the shrimps by digging out their burrows with a shovel down to about 40 cm at low water spring tide from April 1997 to May 1999 (Table 1). For each shrimp collected, the species, sex, body length, carapace length (including rostrum), and the presence or absence of a symbiotic bivalve were recorded. For shrimps harboring a bivalve, the attachment site, length, and lateral diameter of the shell was measured. We compared these morphological characters with those specimens of *P. ohshimai* attached to *Upogebia major* (De Haan, 1839) collected at Aio, Ogouri, Yamaguchi Prefecture, Japan, during 20–22 September 1994 (Kato and Itani 1995).

The symbiotic bivalves and their host shrimps were fixed in 70% ethanol or 10% formalin and dissected for anatomical investigation.

Results

Upogebia carinicauda was found in high densities on the tidal flat at Ashiken, Amami-Oshima Island. Of the 422, 120, and 95 shrimps collected on 22 June 1997, 13 December 1997, and 17 February 1999, respectively, 18 (4.3%), 2 (1.7%), and 2 (2.1%) harbored symbiotic bivalves (Table 1). The bivalves proved to belong to a new species of the genus *Peregrinamor*, which is described below.

Peregrinamor gastrochaenans n. sp.

Materials examined. Holotype (Fig. 2A, B): No. 3, 6.4 mm [shell length]. Paratypes (5): No. 4, 5.8 mm; No. 7 (Fig. 1A, B), 4.3 mm; No. 15, 3.2 mm; No. 16, 5.3 mm; No. 17, 4.5 mm.

Total materials: 18 specimens, Ashiken, Amami-Oshima Is., 22 June 1997 (Nos 1–18, including 6 type specimens); 2 specimens, Ashiken, 13 December 1997 (Nos 19, 20); 2 specimens, Ashiken, 17 February 1999; 1 specimen, Kuba, Amami-Oshima Is., 20 June 1997; 1 specimen, Kuba, 13 May 1999; 1 specimen, Uken, Amami-Oshima Is., 22 June 1997.

Table 1. Sites of tidal flats surveyed for symbiotic bivalves of *Upogebia* shrimps, with numbers of hosts examined and symbionts detected.

Site	Island	Date	Number of <i>Upogebia</i>	Number of <i>Peregrinamor</i>	% symbiosis
Ashiken	Amami-Ohshima	22 Jun. 97	422	18	4.3
		13 Dec. 97	120	2	1.7
		17 Feb. 99	95	2	2.1
Kuba	Amami-Ohshima	2 Apr. 97	115	0	0.0
		20 Jun. 97	192	1	0.5
		12 Dec. 97	91	0	0.0
		13 May 99	135	1	0.7
Uken	Amami-Ohshima	22 Jun. 97	68	1	1.5
Yanyuu	Amami-Ohshima	20 Jun. 97	112	0	0.0
		13 Dec. 97	82	0	0.0
Miura	Kakeroma	23 Jun. 97	214	0	0.0

Type materials are deposited in the Kyoto University Museum (Nos 3, 16, and 17) and in the Seto Marine Biological Laboratory, Kyoto University (Nos 4, 7, and 15; SMBL Type No. 394).

Type locality. Tidal flat at Ashiken, Uken-son, Ohshima-gun (Amami-Ohshima Island), Kagoshima Prefecture, Japan, 28°17'N, 129°16'E.

Diagnosis. Shell small, mytiliform, laterally inflated, much compressed dorso-ventrally, ventral side flattened. Shell having small gape at antero-ventral corner of valves, from which edges of the mantle protrude to form anterior inhalant siphon. Ventral side of shell having large posterior gape, from which expanded mantle protrudes.

Description. Animal symbiotic, firmly attached by byssus to ventral side of cephalothorax of mud shrimp *Upogebia carinicauda*. Occurring singly with dorso-ventral and longitudinal orientation, with its anterior part towards host's head (Fig. 1A, B).

Shell length 6.4 mm, height 2.3 mm, breadth 4.4 mm (holotype). Shell very thin and fragile, dorso-ventrally flexible, greatly inflated laterally and much depressed dorso-ventrally, more strongly compressed towards umbo, so outline of the shell ovoid in dorsal and ventral aspects (Figs 1D, E, 2A, B). Reniform in lateral view (Fig. 1C); beaks situated at anterior termination, widely separated from each other, not leaving a concave area between them. Anterior end of shell compressed, roundly truncated; posterior end also compressed, obliquely truncated. Ventral side flattened, occasionally decalcified and softened, with periostracum imprinted by surface structure of ventral side of host's cephalothorax.

Valve margins meeting only antero-ventrally; leaving small gape at antero-ventral corner and large postero-ventral gape (Fig. 1F, G). When young, however, shell less inflated laterally, and postero-ventral gape absent or narrow.

Hinge edentulous, but with ill-defined knob-like process just in front of ligamental groove (Fig. 1H, I). Ligament bridged transversely between umbos.

Periostracum thin, grayish yellow. Interior of shell grayish white. Cavity deep with weakly developed septum inside anterior end, on which anterior adductor is seated; small retractor muscle scar on hind part of ligamental groove; and small,

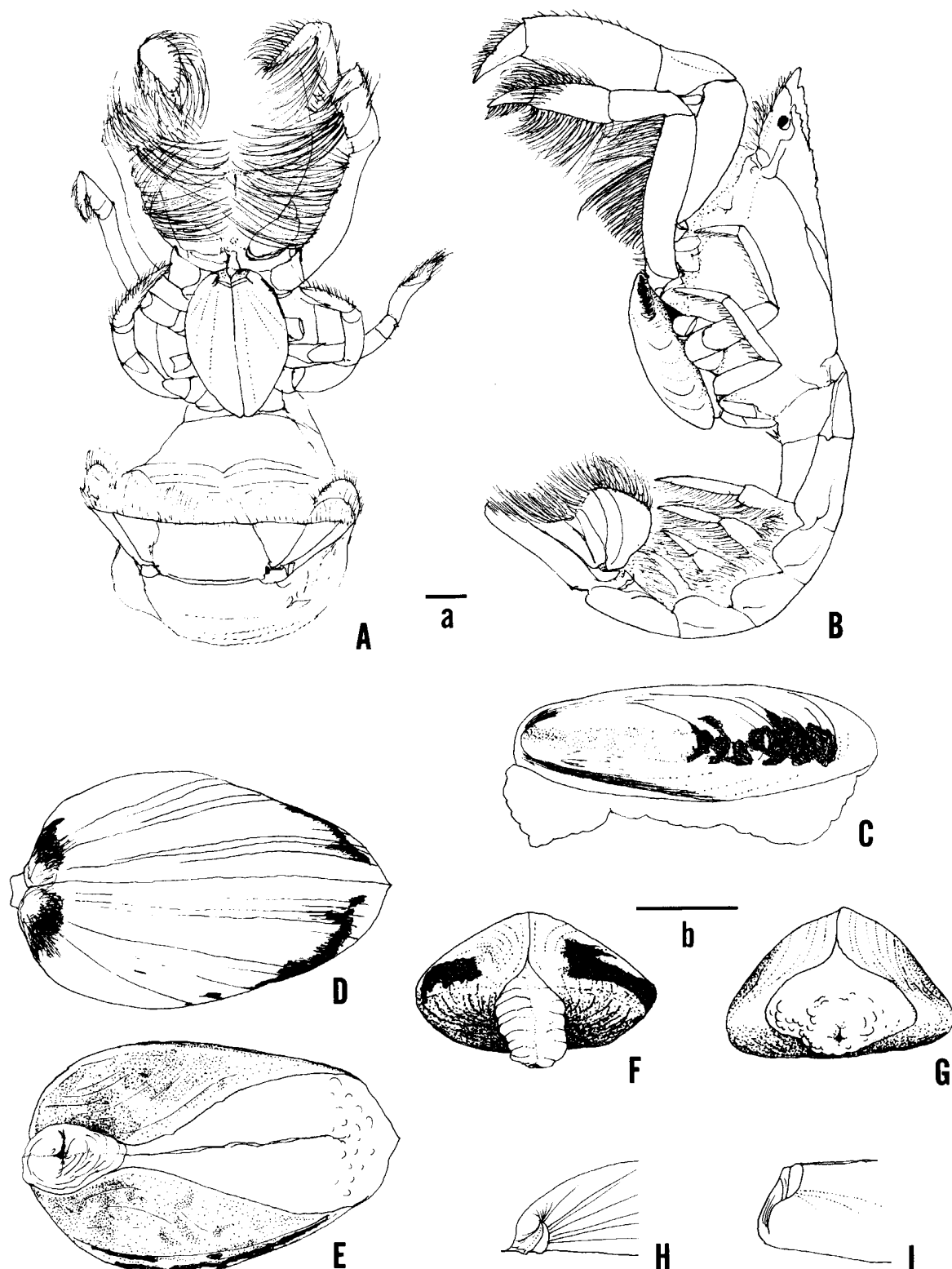


Fig. 1. A symbiotic bivalve, *Peregrinamor gastrochaenans* n. sp., and its host shrimp, *Upogebia carinicauda*. A, B, ventral and lateral postures, respectively, of the symbiotic relationship (paratype, No. 7); C–G, lateral, dorsal, ventral, anterior, and posterior views, respectively, of a bivalve (No. 18); H, I, dorsal and inner lateral views, respectively, of a right shell (No. 19). Scale bars=1 mm; a, for A and B, b, for C–I, respectively.

obsolete posterior scar at the posterior end near margin.

Body compressed dorso-ventrally; dorsal side flat. Mantle opened in two places, anterior opening (pedal) and narrow posterior opening (exhalant) (Fig. 1E, G). Pair of vigorously contractile (in life) edges of mantle protruding from antero-ventral shell gape, forming inhalant siphon (Fig. 1E, F). Postero-ventral part of mantle expanded and fleshy, protruding from large postero-ventral shell gape (Figs 1D, G, 2C).

Foot long, rod-like, with well-developed byssal gland; opening of latter in form of longitudinal groove. Both anterior and posterior adductors nearly equal in size (isomyarian); retractors in two pairs. Mouth opening between two pairs of labial palps. Labial palp-ctenidial junction of category 3 (cf. Stasek 1963). Basic structure of organs of pallial cavity similar to that of *P. ohshimai* (Shôji 1938). Livers paired, dendriform, their lobes filling whole space around stomach, sending pair of hepatic ducts to cardia. Kidney elongate, sacciform.

Gills in two pairs joined anteriorly with external and internal labial palps respectively; outer demibranch snaptorhabdic, rather vestigial, being a mere fold formed inside mantle; inner demibranch homorhabdic, reticular, divided into ascending and descending filaments, forming between them a space, the supra-branchial cavity.

Hermaphroditic or gonochoristic; ovaries forming net-work, filling not only most of visceral sac but also extending into tissues of mantle; ovaries housed in postero-ventral part of mantle sometimes protruding laterally from gape between shells.

Larvae and dividing eggs found in supra-branchial cavity (brood-chamber), sometimes showing various stages of development (Fig. 2D). Small shelled juveniles occasionally found attached to ventral shell margin of brooding bivalves (Fig. 2D) or to ventral side of host's cephalothorax.

Distribution. Only known from Amami-Ohshima Island, Japan.

Etymology. From Greek *gaster* (stomach, belly) and *chaino* (open, gape), participle, from the large postero-ventral gape between the valves, and also indicating the superficial resemblance of the shells to those of *Gastrochaena* (Gastrochaenidae), whereas the gape of *Gastrochaena* is in an antero-ventral position (Carter 1978).

Japanese name. Shimanohate-magokorogai

Ecology and behavior. There is no overlap in distribution or host species between the two species of *Peregrinamor*; *P. gastrochaenans* is known only from *Upogebia carinicauda* in the Amami Islands while *P. ohshimai* is known from *U. major*, *U. yokoyai* Makarov, 1938, *U. issaeffi* (Balss, 1913), and *U. narutensis* Sakai, 1986 in main islands of Japan (Shôji 1938; Sakai 1968; Sakai *et al.* 1995; Kato and Itani 1995) and from *U. major* in China (Bernard *et al.* 1993).

Peregrinamor gastrochaenans grows at a similar rate with its host, maintaining the ratio of shell length to host's carapace length as in *P. ohshimai*. The bivalves are slender when young, but soon become laterally inflated with growth.

In a glass tube in an aquarium, the host shrimp creates water currents by intermittent beating of the pleopods. While the pleopods beat, the first and second pereopods, which are fringed with long ventral setal rows, are pressed against the side walls, and accordingly a filtering basket is formed. Suspended matter in the water current is intercepted by the setae of the basket and swept out with the max-

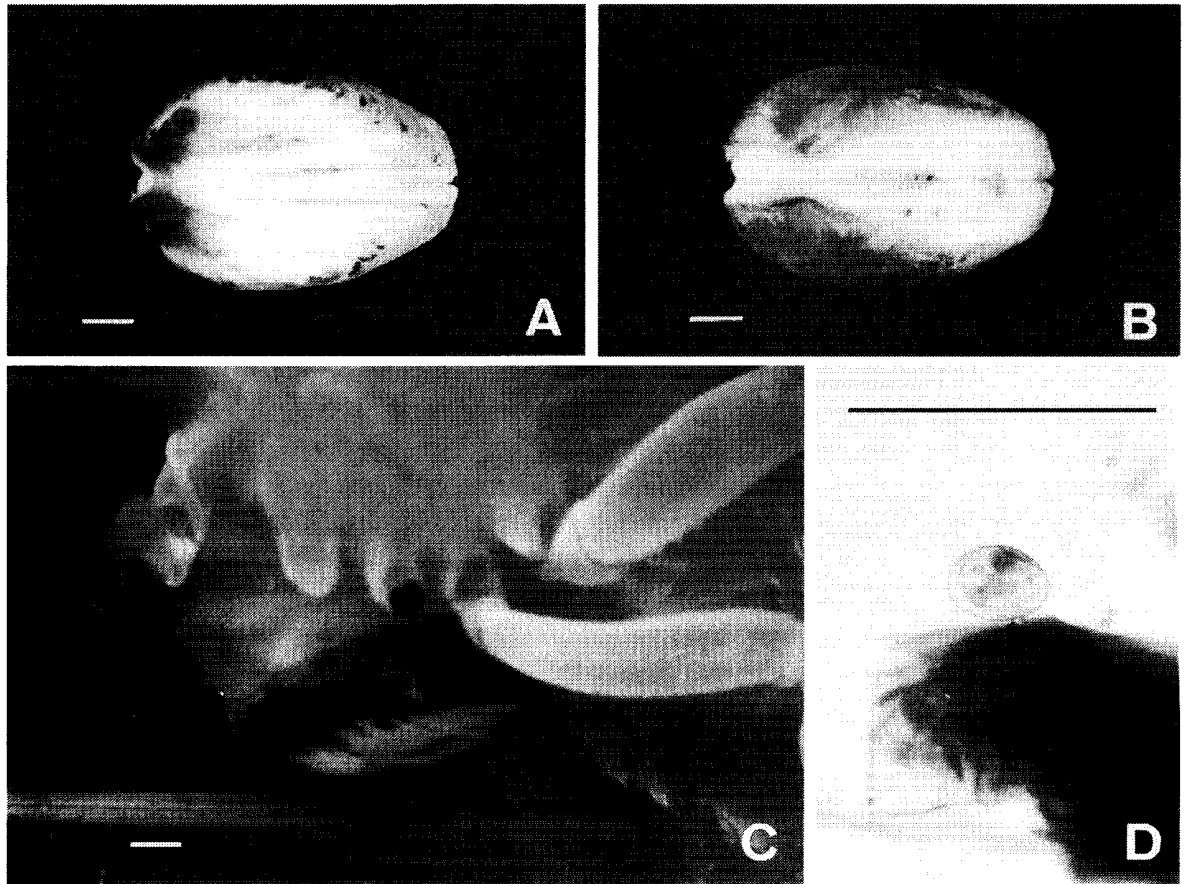


Fig. 2. *Peregrinamor gastrochaenans* n. sp. A, B, dorsal and ventral views, respectively, of an ethanol-preserved specimen (holotype); C, lateral view of a living bivalve (No. 19) attached to its host shrimp, *Upogebia carinicauda*; D, a juvenile attached to the ventral side of an adult, whose supra-branchial cavity is full of veliger larvae. Scale bars=1 mm.

illipeds. The symbiotic bivalve extends the vigorously contractile anterior edges of the mantle from the anterior small gape of the shell and inserts them into the host's filtering basket, forming an inhalant siphon. The exhalant aperture formed by the posterior part of the bivalve's mantle also opens. Like *P. ohshimai*, the new bivalve proceeds to pilfer suspended matter intercepted by the host's filtering basket.

Discussion

The only species so far known in the galeommatoidean genus *Peregrinamor* is *P. ohshimai*, which is known only from temperate tidal flats (Shôji 1938), and from large- and middle-sized *Upogebia* species as hosts, e.g., *U. major* and *U. narutensis*, and *U. yokoyai* and *U. issaeffi*, respectively (Kato and Itani 1995). The new species described in this paper is interesting, because it is the first species of the genus found from subtropical waters and because it has a symbiotic relationship with small species of *Upogebia*. This new species, *P. gastrochaenans*, has basically similar morphological characters and ecological properties as *P. ohshimai*, but it can

be discriminated from the latter by its laterally more inflated shell with a permanent ventral gape, and by the expanded, fleshy posterior mantle protruding from the gape.

The host shrimps often use their telsons to beat and press their symbiotic bivalves against the ventral side of the cephalothorax. The expanded, fleshy mantle protruding from the wide postero-ventral shell gape might function as a cushion to prevent the shells and visceral mass from being smashed, and it may also sometimes function as a "spare pouch" housing expanded ovaries.

The bivalve grows at a similar rate with its host, maintaining the ratio of shell length to host's carapace length as in *P. ohshimai*. This suggests that the bivalve can relocate to a newly molted shrimp after ecdysis, and that the energy obtained by the bivalve by pilfering its host's filtering basket for food is enough to maintain the same relative size as the host grows. Any surplus energy obtained by the bivalves should be allocated to reproduction, because deviating from the constant host-symbiont size ratio as a result of overgrowth will increase mortality. Long-duration reproduction and larval brooding have been observed in many galeommatoid bivalve species that have ecto-symbiotic (Morton 1972; O'Foighil and Gibson 1984; O'Foighil 1985), endo-symbiotic (Kato 1998), or burrow-symbiotic (Mikkelsen and Bieler 1989) relationships with various invertebrates, and their growth maintains the host-symbiont size ratio.

Both species of *Peregrinamor* start to reproduce when they are still young (see Kato and Itani 1995 for *P. ohshimai*). To maximize lifetime fitness, bivalves whose hosts are small and probably short-lived should start reproduction earlier, because late reproduction will increase mortality. Both species are slender when young, but soon they become laterally inflated with growth, presumably reflecting the development of ovaries. The change in shell shape occurs at an earlier stage in *P. gastrochaenans* than in *P. ohshimai*, as predicted, probably because the host's adult size is much smaller in the former.

Both species of *Peregrinamor* have similar feeding habits, attaching themselves to the ventral side of the cephalothorax of the host shrimp and pilfering suspended matter intercepted by the host's filtering basket. However, it is still unknown whether the bivalve is commensal, parasitic, or mutual. The effects of the symbiotic bivalves upon host shrimps, in comparison to conspecific shrimps from the same sites that lack bivalves, have not yet been quantified. Furthermore, it is necessary to compare the size distribution of particles filtered by the host's filtering basket with those filtered by the bivalve's ctenidia.

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